[The Great Lakes Entomologist](https://scholar.valpo.edu/tgle)

Volume 45
Numbers 1 & 2 - Spring/Summer 2012 *Numbers 1 & 2 - Spring/Summer 2012*

Article 6

April 2012

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Alan Molumby
University of Illinois

Tomasz Przybylowicz
University of Illinois

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Alan Molumby[1] and Tomasz Przybylowicz[1]

Abstract

Bees (Hymenoptera: Apoidea) were collected at 24 sites chosen to represent the diversity of urban and natural habitats in the Chicago metropolitan area. Species richness was assessed for each site. Patterns of habitat use were inferred from collection records. In urban areas, we collected 33 species, belonging to 15 genera and 5 families. Areas of preserved natural habitat yielded 44 species, in 20 genera, and 6 families. Twenty species were common to both urban areas and areas of preserved natural habitat. Species at each site were ranked by the number of times they were collected. The bees most often collected in urban areas were widely-distributed species documented in other urban areas. Areas of preserved natural habitat harbored a higher richness of species, and the species most-often collected in these areas were native to North America. Urban sites with native plant species harbored significantly more bees than urban sites lacking native vegetation (t-test, two-tailed assuming unequal variances, $P < 0.001$). In urban areas, native bees were more likely to be captured on native flowers (c^2, Yates statistic, $P < 0.01$). Chicago's bee fauna is comparable in richness to the bee fauna of other cities which have been surveyed, notably Phoenix, AZ (Mc Intyre and Hostelter 2001), Berkeley, CA (Frankie et al. 2005), and New York City, NY, (Matteson et al. 2008). A comparison of our species list to another, recently-published survey of Chicago bees by Toinetto et al. (2011), revealed only 24 species overlap, from a combined total list of 93 species. The combined species list from these two surveys shares only 44 species in common with the 169 species documented by Pearson (1933) in his extensive survey of Chicago bees.

To the creatures that inhabit them, urban landscapes pose distinctive ecological challenges and rewards. Worldwide, increasing urbanization has created progressively larger cityscapes, while simultaneously fragmenting the natural habitats that formerly surrounded these areas of urban development. With urbanization comes a cascade of habitat changes, each with the potential to affect wildlife populations (Theobald et al. 1997). Dedicated natural areas adjacent to cities have been fragmented into islands, surrounded by a matrix of urbanized and partially urbanized habitat (Dickman 1987). As this process continues, a progressively larger fraction of the world's biological communities experiences some degree of urbanization.

The implications of this process are twofold. Typically, urban areas harbor a distinctive fauna of species adapted to, or tolerant of, the challenges of urban life (Crooks 2002). Urban areas provide abundant resources for certain species able to remove themselves from their original ecological context by adapting to life in urban settings. These species are almost inevitably disturbance-tolerant ecological generalists- and are often cosmopolitan or widespread in their distri-

[1]University of Illinois at Chicago, Department of Biology, 845 West Taylor Street, Chicago, IL 60607.

bution. Worldwide, the urban matrix supports a large number of these species, some at densities much higher than they would normally occur in wild communities (Brady and Altizer 2007).

A probable global decline in the density and diversity of pollinating species, the "pollination crisis" (Buchanan and Nabhan 1997, Allen-Wardell et al. 1998, Kearns et. al. 1998, Biesmeijer et al. 2006, but see Ghazoul 2005), has heightened interest in the ecological status of pollinator guilds worldwide. Dramatic declines in North American populations of the introduced honeybee, *Apis mellifera* L., have threatened major economic losses to agriculture (Allen-Wardell et al. 1998), underscoring the need for pollinator conservation, and incited renewed interest in the continent's autochthonous bees.

Habitat fragmentation is not likely to be a new phenomenon for bees (Cane 2001). Given that the nesting substrates and flowers bees need to survive are often ephemeral in nature, many or most species of bees may have historically existed as metapopulations, matrices of individually unstable populations maintained by a balance of extinction and recolonization. A reduction in the size or density of these suitable areas of habitat space is likely to cause the extinction of species from the system as a whole, because metapopulations have minimum viable sizes (Hanski et al. 1996). As localized areas of suitable habitat shrink, their equilibrium species richness should decline, and the landscape as a whole might be expected to loose species. Urban landscapes might also alter the dynamics of neighboring natural areas by providing a reservoir of ecological generalists, some of which are able to invade local areas of preserved habitat and prevent their recolonization by locally extinct bees with similar resource use but greater degrees of ecological specialization. Localized extinction of species in a nature preserve imbedded in cityscape could be followed by recolonization from populations of these same species located elsewhere. Alternatively, lost species could be replaced by ecologically similar species tolerant of urban landscapes. Habitat fragmentation has been demonstrated to favor some species of bees over others. For instance, the clearing of forests in Argentina has created widespread ecological changes, favoring the introduced honeybee, *A. mellifera*, over native pollinators (Aizen and Feinsinger 1994). The urban matrix surrounding a natural area is bound to exert an influence on the types of species that are able to invade and establish themselves in these habitat fragments, acting as a biological filter for potential colonists.

Because of their importance to biological communities, it is of no small importance that we understand the impact of urbanization on bees. Several studies have established the importance of natural habitat for the maintenance of bees valuable to conservation (Banaszak 1992, Greenleaf and Kremen 2006). In terms of the bigger picture, the pollination services of bees are essential to the functioning of most terrestrial ecosystems, and studies have raised concern that many bee species are in decline. An extensive study of the European bee fauna by Biesmeijer et al. (2006) suggests that oligolectic, non-vagile, univoltine, and habitat-specializing species, are particularly prone to decline due to anthropogenic habitat change.

Urban bees may be an assemblage of disturbed-habitat species opportunistically able to exploit the urban environment, native species en route to colonize fragmented natural habitat, or some combination of the two. Certain bees are abundant in cities (McIntyre and Hostelter 2001, Frankie et al. 2005, Cane et al. 2006, Matteson et al. 2008). A survey of the Northern California cities of Berkeley and Albany noted 74 different species of bees (Frankie et al. 2005). Native plant cultivars harbored many native bees as visitors. This was also found to be the case in Phoenix, AZ, where the highest densities of bees were found in areas of native, xeric vegetation, planted within urbanized landscapes. This suggests urban areas have the potential to act as refugia for bee species that have suffered loss of habitat due to human activity, and also that certain urban landscapes may act as habitat corridors for bees as they travel between remnants of natural vegetation. In contrast, a bee survey of New York City community gardens reported large numbers of exotic species (Matteson et al. 2008).

It is possible that the differences in bee fauna between these cities can be attributed to differences in the urban landscapes themselves, suggesting that there is a great deal to be learned about how bees interact with the resources offered up to them by human-dominated environments. The aims of this study were 1) to characterize the urban bee assemblages of Chicago, Illinois with those of the natural areas surrounding it, 2) to identify aspects of habitat use which enable some species to become common in urban areas and allow others to use urban areas as migration corridors to areas more suited to their needs.

Materials and Methods

Bees were collected, over the eight growing seasons (April to September), from 2002 to 2009. Collections were made at sites in metropolitan Chicago, its suburbs, forest preserves in Cook County, and the Indiana Dunes National Lakeshore. Specimens were collected using an insect net while bees were visiting flowers or, in the case of some male specimens, defending territories. Bee bowls were not used for collecting. Collected specimens were pinned and mounted, and identified by Alan Molumby. Assistance in identifications was provided as needed by Dr. Elizabeth Day or Dr. Mike Arduser.

Study Sites. Study sites are listed in Table 1. The sites we chose fell into two general categories: areas of preserved natural habitat, defined as those sites that are located within the boundaries of a dedicated conservation area, and "urban" areas, defined as those sites that are located within the bounds of private or public property dedicated to uses other than conservation. All the sites in this latter category were areas dominated by human urban or suburban development, such as railroad margins, ornamental gardens, or the like.

Areas of preserved natural habitat included sites within the Cook County Forest Preserve and Indiana Dunes National Lakeshore, and the Woodworth Prairie, a prairie remnant overseen by the University of Illinois at Chicago (UIC). The sites were chosen to represent a diverse collection of the natural habitats that have survived in the wake of the urban expansion of the Chicago, Hammond, and Gary metropolitan areas, albeit with varying degrees of anthropogenic influence. These habitats include mesic tallgrass prairie (the Woodworth Prairie), savannah with scattered green ash trees (Bunker Hill), mixed deciduous forest (all three essentially floodplain forests, located at Thatcher Woods, Harms Woods, and Spears Woods), marsh (Calumet Trail), bog (Pinhook Bog), successional oak forest (House Site, Indiana Dunes), and dunes (Kemil Beach, Ogden Beach, Mount Baldy).

Urban sites were chosen at various locations in Chicago and its nearby suburbs, to represent a diversity of urban habitats. These included a dedicated prairie garden used for teaching (UIC Greenhouse), a backyard garden with native plants (Molumby Garden), a very large urban garden for ornamentals (the Lurie Garden), various plots used for private and public landscaping (i.e., the Art Institute, North and Hermitage, Wicker Park, UIC Landscaping), open lots (West Loop), and railroad margins (Hubbard and Ogden, Chicago Honey Co-op). Some of these urban sites harbored significant numbers of native plant species important to the needs of native bees (Lurie Garden, Molumby Garden, UIC Greenhouse, Hubbard and Ogden), others contained almost entirely non-native species typical of disturbed habitats, garden cultivars which were either nonnative (i.e., catnip, *Nepeta catara (*L.)), modified very significantly from their wild growth form by artificial selection, or both. Urban sites were classed as harboring native vegetation if, during any collecting trip, flowering native plants could be located.

Table 1. Names, Habitat Type, Latitude/Longitude, Vegetation, and Species Richness of the Field Sites Sampled for this Study.

Name	Urban vs. Natural	Habitat Type	Latitude/Longitude	Native Plants?	Species Richness	Collecting Visits	Specimens Collected
UIC Greenhouse	Urban	Garden	41.869273°N, 87.646437°W	Yes	20		50
Hubbard and Ogden	Urban	Railroad Margin	41.890170°N, 87.659333°W	Yes	12	11	24
Molumby Garden	Urban	Garden	41.897230°N, 87.774045°W	Yes	21	16	41
River Forest Garden	Urban	Garden	41.907867°N, 87.818270°W	No	1	4	5
Art Institute of Chicago	Urban	Landscaping	41.879547°N, 87.623799°W	No	6	3	6
Lurie Garden	Urban	Garden	41.881001°N, 87.621803°W	Yes	11	6	22
UIC Landscaping	Urban	Landscaping	41.872022°N, 87.647767°W	No	5	4	5
Wicker Park	Urban	Garden	41.907643°N, 87.676263°W	No	7	3	7
West Loop	Urban	Railroad Margin	41.888597°N, 87.655438°W	No	6	4	7
West Side	Urban	Railroad Margin	41.868346°N, 87.728169°W	No	3	3	13
North and Hermitage	Urban	Landscaping	41.910821°N, 87.671156°W	No	3	3	4
Calumet Trail	Natural	Marsh	41.642452°N, 87.078195°W	Yes	10	3	17
Thatcher Woods	Natural	Mixed Deciduous Forest	41.895186°N, 87.832088°W	Yes	3	3	11
Spears Woods	Natural	Mixed Deciduous Forest	41.726166°N, 87.854362°W	Yes	3	3	4
Harms Woods	Natural	Mixed Deciduous Forest	42.072934°N, 87.773252°W	Yes	16	8	23
Bunker Hill	Natural	Savannah	42.008872°N, 87.788143°W	Yes	21	9	35
Woodworth Prairie	Natural	Mesic Tallgrass Praire	42.059497°N, 87.841970	Yes	12	5	21
Ogden Beach	Natural	Dunes	41.625644°N, 87.202349°W	Yes	10	4	10
Mount Baldy	Natural	Dunes	41.657940°N, 87.057037°W	Yes	2	3	2
Pinhook Bog	Natural	Bog	41.615040°N, 86.848359°W	Yes	5	4	6
Beverly Shores Road	Natural	Successional Oak Forest	41.701948°N, 86.939428°W	Yes	3	3	4
House Site, Indiana Dunes	Natural	Successional Oak Forest	41.630071°N, 87.091026°W	Yes	17	5	21
Kemil Beach	Natural	Dunes	41.661723°N, 87.065620°W	Yes	4	3	4
Miller Beach	Natural	Dunes	41.615571 °N, 87.271614°W	Yes	3	3	4

The area of contiguous bee habitat within each of these sites is not known to us currently, but for each site, collections were made along a transect of 10-100 meters, following a dedicated trail, path, or sidewalk. Collections were made at various times of day, especially mid-late afternoons, on sunny days, when the widest diversity of bees were active. For each site, multiple collections (at least three, up to ten or more) were made, at different times of year, and over the course of several years. Visual sightings of bees were not included in the data sets used for this study.

Species lists were compiled for each site, for areas of preserved natural habitat vs. "urban" sites overall, and for all sites combined. The number of instances each species was collected, and the number of sites at which that species occurred, were noted. The former statistic was transformed into a numerical rank to provide a rough index of relative abundance. Nesting sites and diet of each species was established from the literature, and from our own observations of the bees. Bees were evaluated in terms of their nesting substrate, their diet (oligolecithic bees that collect pollen from only one species or a restricted set of species vs. polylecithic bees that collect pollen from a wide variety of flowering species), their phenology (univoltine species present in spring or in late summer vs. multivoltine present throughout the growing season), their social behavior (eusocial, primitively social, solitary), and whether or not they are native to North America.

Data Analyses. For urban sites, the species richness of sites harboring native plants was compared to that of sites lacking native vegetation using a Student's *t*-test.

Habitat use patterns of native bees in urban areas were assessed, using plant identifications from bees captured in the process of foraging. Flowers on which bees were collected were classed as either "native" or "non-native" based upon whether the species occurs naturally in the Chicago region. A 2 × 2 contingency table was constructed, to test whether the occurrence of native vs. exotic bees was independent of whether the flower was native or nonnative.

Comparison with Other Faunal Surveys. Our species list was compared with a species list from a recently published survey of Chicago-Area bees by Tonietto et al. (2011). For comparison, ambiguous specimens (i.e., those listed as *Hylaeus affinis* (Smith) or *Hylaeus modestus* Say) were excluded from the Tonietto et al. (2011) list. The remaining entries were compared, and a combined species list from the two surveys was generated. This combined list was similarly compared to the species list published by Pearson (1933) in his extensive survey of Chicago-area bees. Many of the scientific names used by Pearson (1933) are now obsolete and were updated to current nomenclature for purposes of comparison.

Results

Composition of bee fauna. An inventory of the bees collected to date is presented in Table 2. In urban areas, we collected 33 species, belonging to 15 genera and 5 families. The various areas of preserved habitat we sampled yielded 44 species, in 20 genera, and 6 families, with 20 species shared between them.

The habitats we sampled differed greatly in their species richness and diversity. Species lists for each habitat, ranked by the number of times each species was collected, are presented in Tables 3 and 4. Some species were restricted to a single habitat or collection site, but others were present across a wide range of habitats. This was the case in both urban habitats and preserved natural habitats. Figure 1 shows the number of species collected versus the number of sites at which they were collected. The exotic species, *A. mellifera*, *Anthidium manicatum* (L.), and *Megachile rotundata* (Fabricius) were the most commonly

Table 2. Bee species collected in this study.

Family	Species	Number Collected	Number of Sites	Native vs. Exotic	Nest Substrate	Pollen Specificity	Social Behavior	Phenology
Andrenidae	*Andrena crataegi* Robertson	1	1	N	Sand/Soil/Clay	Poly	Communal	Early
Andrenidae	*Andrena cressonii* Robertson	5	1	N	Sand/Soil/Clay	Poly	Solitary	
Andrenidae	*Andrena distans* Provancher	2	1	N	Sand/Soil/Clay	Oligo (wild geranium)	Solitary	Early
Andrenidae	*Andrena dunningi* Cockerell	4	2	N	Sand/Soil/Clay	Poly	Solitary	Early
Andrenidae	*Andrena imitatrix* Cresson	2	2	N	Sand/Soil/Clay	Poly	Solitary	Early
Andrenidae	*Andrena mandibularis* Robertson	1	1	N	Sand/Soil/Clay	Poly	Solitary	Early
Andrenidae	*Andrena nivalis* Smith	2	2	N	Sand/Soil/Clay	Poly	Solitary	Early
Andrenidae	*Andrena wheeleri* Graenicher	3	2	N	Sand/Soil/Clay	Oligo (umbellifers)	Solitary	Early
Andrenidae	*Andrena wilkella* (Kirby)	2	1	N	Sand/Soil/Clay?	Poly (Slightly Oligo on Fabaceae)	Solitary	EarlyMid
Apidae (Anthophorini)	*Anthophora terminalis* Cresson	2	2	N	Soil?	Poly	Solitary	MidLate
Apidae (Anthophorini)	*Melissodes agilis* Cresson	6	4	N	Soil	Moderately Oligo (*Helianthissp.*)	Solitary	MidLate
Apidae (Anthophorini)	*Melissodes bimaculata* (Lepeletier)	7	4	N	Wood Pulp	Poly	Solitary	MidLate
Apidae (Anthophorini)	*Melissodes druriella* (Kirby)	5	3	N	Soil	Somewhat Oligo (Solidago, Aster, compositae)	Solitary	MidLate
Apidae (Anthophorini)	*Melissodes subillata* LaBerge	2	1	N	Soil	Poly	Solitary	MidLate
Apidae (Anthophorini)	*Melissodes tincta* LaBerge	1	1	N	Soil	Oligo (compositae, Chrysopsis and Aster)	Solitary	Late

Table 2. Continuted.

Family	Species	Number Collected	Number of Sites	Native vs. Exotic	Nest Substrate	Pollen Specificity	Social Behavior	Phenology
Apidae (Anthophorini)	*Melissodes trinodis* Robertson	4	2	N	Soil	Slightly Oligo (compositae, *Helianthis*)	Solitary	Late
Apidae (Anthophorini)	*Peponapis pruinosa* (Say)	2	1	N	Soil	Oligo (*Curcurbita* and *Pontederia*)	Solitary	MidLate
Apidae (Nomadini)	*Nomada depressa* Cresson	3	2	N	*Andrena* nests	Parasite		Early
Apidae (Nomadini)	*Nomada sulphurata* Smith	2	1	N	*Andrena* nests	Parasite		Early
Apidae (Corbiculata)	*Apis mellifera* L.	39	15	E	Nest boxes and cavities	Poly	Advanced Eusocial	All
Apidae (Corbiculata)	*Bombus bimaculatus* Cresson	14	9	N	Rodent burrows	Poly	Social	All
Apidae (Corbiculata)	*Bombus fervidus* (Fabricius)	3	2	N	Underground cavities/woodpiles	Poly	Eusocial	All
Apidae (Corbiculata)	*Bombus griseocollis* (DeGeer)	6	4	N	Underground cavities	Poly	Eusocial	All
Apidae (Corbiculata)	*Bombus impatiens* Cresson	20	10	N	Underground cavities	Poly	Eusocial	All
Apidae (Xylocopinae)	*Ceratina dupla* Say/*calcarata* Robertson complex	9	5	N	Wood Holes	Poly	Solitary	All
Apidae (Xylocopinae)	*Ceratina strenua* Smith	10	4	N	Wood Holes	Poly	Solitary	All
Apidae (Xylocopinae)	*Xylocopa virginica* (L.)	14	14	N	Wood Holes	Poly	Solitary	All
Colletidae	*Colletes thoracicus* Smith	1	1	N	Sand specialist	Poly	Early	Early
Colletidae	*Hylaeus affinis* (Smith)	13	5	N	Twigs	Poly	Solitary	All
Colletidae	*Hylaeus annulatus* (L.)	1	1	E	Twigs	Poly	Solitary	All
Colletidae	*Hylaeus modestus* Say	7	5	N	Twigs	Poly	Solitary	All
Halicitidae	*Agapostemon splendens* (Lepeletier)	1	1	N	Sand	Poly	Solitary	All

Table 2. Continued.

Family	Species	Number Collected	Number of Sites	Native vs. Exotic	Nest Substrate	Pollen Specificity	Social Behavior	Phenology
Halicitidae	*Agapostemon virescens* (Fabricius)	5	5	N	Sand	Poly	Solitary	All
Halicitidae	*Augochlora pura* (Say)	7	7	N	Rotten Wood	Poly	Subsocial	All
Halicitidae	*Augochlorella aurata* (Smith)	3	2	N	Sand	Poly	Subsocial	All
Halicitidae	*Dieunomia heteropoda* (Say)	1	1	N	Sand	Poly	Solitary	Late
Halicitidae	*Dufourea novaeangliae* (Robertson)	1	1	N	Sand	Poly	Solitary	All
Halicitidae	*Halictus confusus* Smith	3	2	N	Sand	Poly	Socially Polymorphic	All
Halicitidae	*Halictus ligatus* Say	12	7	N	Sand	Poly	Eusocial	All
Halicitidae	*Halictus rubicundus* (Christ)	3	3	N	Sand	Poly	Socially Polymorphic	All
Halicitidae	*Lasioglossum anomalum* (Robertson)	2	2	N	Sand	Poly	Social?	All
Halictidae	*Lasioglossum cressonii* (Robertson)	4	2	N	Sand	Poly	Eusocial	All
Halictidae	*Lasioglossum obscurum* (Robertson)	6	3	N	Sand	Poly	Social?	All
Halicitidae	*Lasioglossum quebecense* (Crawford)	1	1	N	Sand	Poly	Solitary	All
Megachildae	*Anthidium manicatum* (L.)	13	6	E	Wood Holes	Poly	Solitary	All
Megachildae	*Chelostoma philadelphi* (Robertson)	4	4	N	Twigs	Poly	Solitary	Early
Megachilidae	*Heriades carinatus* Cresson	5	4	N	Twigs	Poly	Solitary	All
Megachildae	*Hoplitis spoliata* (Provancher)	5	1	N	Wood Holes	Poly	Solitary	Early
Megachildae	*Megachile centuncularis* (L.)	2	1	Holarctic		Wood Holes	Poly	Solitary
All								
Megachildae	*Megachile mendica* Cresson	1	1	N	Wood Holes	Poly	Solitary	MidLate
Megachilidae	*Megachile montivaga* Cresson	1	1	N	Wood Holes	Poly	Solitary	MidLate
Megachilidae	*Megachile pugnata* Say	5	2	N	Wood Holes	Poly	Solitary	MidLate
Megachilidae	*Megachile rotundata* (Fabricius)	21	9	E	Wood Holes	Poly	Solitary	All
Megachilidae	*Megachile texana* Cresson	1	1	N	Wood Holes	Poly	Solitary	All
Megachilidae	*Osmia cornifrons* (Radoszkowski)	1	1	E	Wood Holes	Poly	Solitary	Early
Megachilidae	*Osmia lignaria* Say	1	1	N	Wood Holes	Poly	Solitary	Early
Megachilidae	*Osmia pumila* Cresson	2	2	N	Wood Holes	Poly	Solitart	Early

Table 3. Bee species by habitat type, ranked by the number of times that species was collected at urban sites.

Railroad Margins Species	Times Collected	**Garden/Landscaping** Species	Times Collected
Apis mellifera	1	*Anthidium manicatum*	1
Megachile rotundata	2	*Apis mellifera*	2
Bombus bimaculatus	3	*Bombus impatiens*	2
Agapostemon virescens	4	*Megachile rotundata*	2
Bombus impatiens	4	*Hylaeus affinis*	3
Melissodes druriella	4	*Megachile centuncularis*	5
Halictus confusus	5	*Xylocopa virginica*	5
Anthidium manicatum	*6*	*Melissodes bimaculatus*	*6*
Bombus griseocolis	*6*	*Megachile pugnata*	*7*
Halictus ligatus	*6*	*Andrena dunningi*	*7*
Lasioglossum anomalum	*6*	*Halictus ligatus*	*8*
Megachile centuncularis	6	*Melissodes trinodis*	*8*
Melissodes agilis	6	*Agapostemon virescens*	*9*
Xylocopa virginica	6	*Heriades carinatus*	*9*
		Hylaeus modestus	*9*
		Hylaeus annulatus	*9*
		Melissodes agilis	*8*
		Hylaeus annulatus	*8*
		Andrena wilkella	*10*
		Bombus bimaculatus	*10*
		Bombus fervidus	*10*
		Bombus griseocollis	*10*
		Melissodes subillata	10
		Peponapis pruniosa	10
		Lasioglossum obscurum	11
		Halictus confusus	11
		Halictus rubicundus	11
		Megachile texana	11
		Dieunomia heteropoda	11
		Melissodes druriella	11
		Anthophora terminalis	11

collected species in urban areas. They were less commonly collected in natural habitats although they were present there. Parasitic bees of the genus *Nomada* (Scopoli), were fairly well-represented at two natural sites; however, they were absent from urban areas. Their hosts, bees of the genus *Andrena* (Fabricius), were far better-represented in areas of preserved natural habitat than in urban areas. Eusocial, corbiculate honeybees and bumblebees were represented at both areas of preserved habitat and urban sites, but were more conspicuous elements of the bee fauna in urban areas. Bees of the tribe Anthophorini (Apidae) were more conspicuous elements of the urban sites we sampled, especially gardens, though they were present in both urban sites and in preserved habitats.

Habitat use. Urban sites with native plant species harbored significantly more bee species than urban sites lacking native vegetation (*t* test, two tailed assuming unequal variances $P < 0.001$). Species richness for bees contrasts sharply between urban sites lacking native plant species and urban sites harboring them (Fig. 2). Native bees were more likely to be captured on native flowers than on nonnative flowers in urban areas (c^2 test, Yates statistic, $P < 0.01$). As

Table 4. Bee species by habitat type, ranked by the number of times that species was collected in natural areas.

Oak Forest		**Mixed Deciduous Forest**		**Prairie/Savannah**		**Dune**		**Wetland**	
Species	**Number Collected**	**Species**	**Number Collected**	**Species**	**Number Collected**	**Species**	**Number Collected**	**Species**	**Number Collected**
Augochlora pura	1	*Lasioglossum obscurum*	*1*	*Bombus bimaculatus*	1	*Xylocopa virginica*	*1*	*Ceratina strenua*	*1*
Bombus griseocollis	2	*Andrena distans*	*2*	*Halictus ligatus*	2	*Melissodes agilis*	*1*	*Ceratina dupla/ calcarata*	*2*
Ceratina dupla/ calcarata	2	*Andrena dunningi*	*2*	*Andrena cressonii*	3	*Megachile mendica*	*2*	*Apis mellifera*	*2*
Halictus rubicundus	2	*Andrena imitatrix*	*2*	*Apis mellifera*	3	*Megachile rotundata*	*2*	*Augochlorella aurata*	*3*
Hylaeus modestus	2	*Andrena mandibularis*	*2*	*Augochlora pura*	4	*Hylaeus affinis*	*2*	*Xylocopa virginica*	*3*
Andrena imitatrix	3	*Andrena wheeleri*	*2*	*Ceratina dupla/ calcarata*	4	*Halictus ligatus*	*2*	*Osmia cornifrons*	*4*
Apis mellifera	3	*Apis mellifera*	*2*	*Chelostoma philadelphi*	4	*Ceratina strenua*	*2*	*Megachile montivaga*	*4*
Bombus bimaculatus	3	*Bombus bimaculatus*	*2*	*Nomada depressa*	4	*Ceratina dupla/ calcarata*	*2*	*Hoplitis spoliata*	*4*
Ceratina strenua	3	*Heraides carinatatus*	*2*	*Nomada sulphurata*	4	*Bombus griseocollis*	*2*	*Bombus impatiens*	*4*
Chelostoma philadelphi	3	*Andrena craetaegi*	*3*	*Lasioglossum obscurum*	4	*Bombus bimaculatus*	*2*	*Osmia pumila*	*4*
Lasioglossum cressonii	3	*Andrena nivalis*	*3*	*Bombus impatiens*	4	*Augochlora pura*	*2*	*Augochlora pura*	*4*
Augochlorella aurata	3	*Augochlora pura*	*3*	*Andrena wheeleri*	5	*Apis mellifera*	*2*		
Melissodes agilis	3	*Hoplitis truncate*	*3*	*Anthophora terminalis*	5	*Agapostemon splendens*	*2*		
Melissodes bimaculata	3	*Hylaeus modestus*	*3*	*Bombus impatiens*	5				
Melissodes tincta	3	*Lasioglossum quebecense*	*3*	*Ceratina strenua*	5				
Xylocopa virginica	3	*Nomada depressa*	*3*	*Dufourea novaeangliae*	5				
		Osmia lignaria	*3*	*Lasioglossum quebecense*	5				
		Osmia pumila	*3*	*Megachile rotundata*	5				
		Xylocopa virginica	*3*	*Anthidium manicatum*	5				
				Bombus fervidus	5				
				Halictus confuses	5				
				Melissodes druriella	5				
				Xylocopa virginica	5				

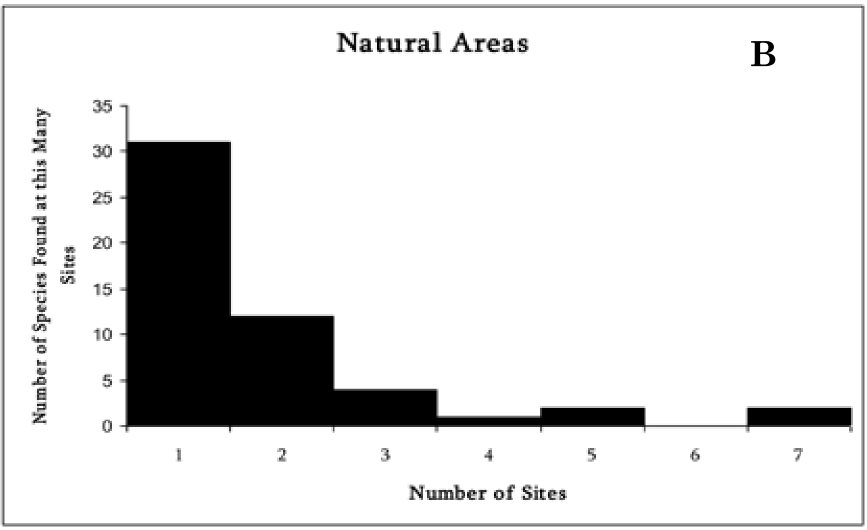

Figure 1. Numbers of bee species vs. occurrence of bee species, expressed as the number of sites at which they were collected, for (A) urban, and (B) natural areas.

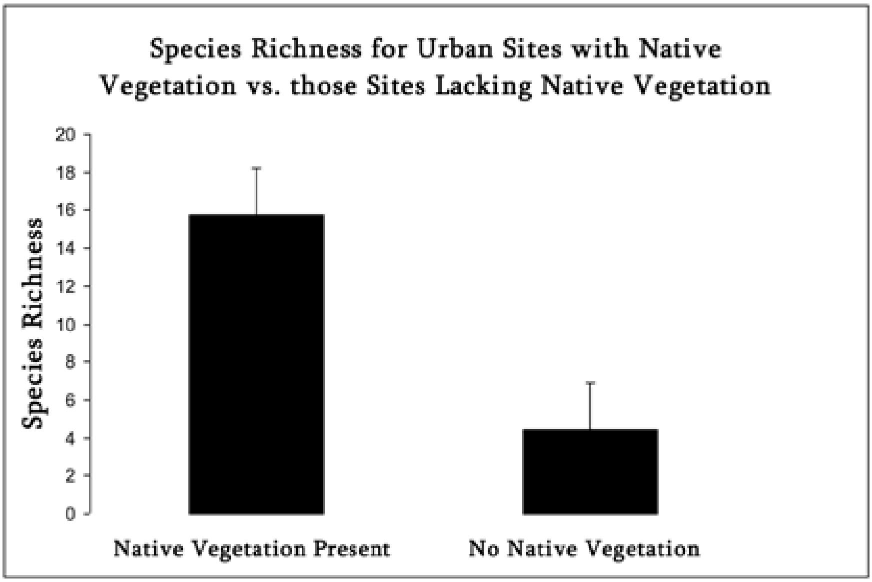

Figure 2. Comparison of species richness for bees collected in urban sites with native vegetation to urban sites with no native vegetation. The height of the bar represents the mean species richness for the sites surveyed, error bars represent standard error of the mean. N = 4 sites with native vegetation and N = 7 sites lacking native vegetation.

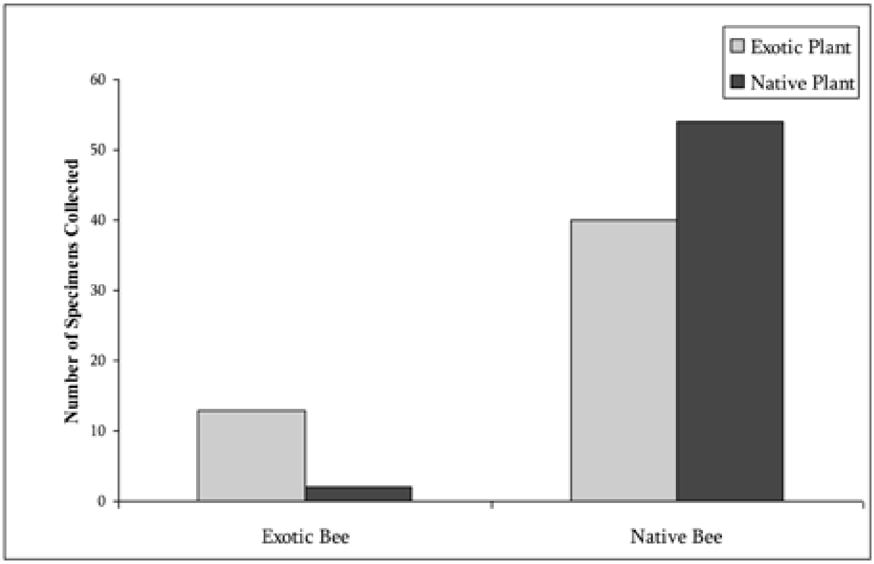

Figure 3. Numbers of native vs. nonnative specimens collected on native vs. exotic flowers in urban areas.

shown in Figure 3, collections from native flowers in urban areas yielded more native bees than exotics, while collections from non-native flowers in urban areas showed the opposite pattern.

Comparison with Other Faunal Surveys. The species list documented in this study shares 24 species with the survey by Tonietto et al. (2011), with 34 species unique to our study and 35 species unique to the Tonietto et al. (2011) study. The combined species list from Tonietto et al. (2011) and this study has 93 species. Table 5 lists species common to Tonietto et al. (2011) and this study. Table 6 lists bee species common to the survey by Pearson (1928) and at least one contemporary survey, either this study or the survey by Tonietto et al. (2011). Pearson documented 125 species in his 1933 survey that were not documented in either contemporary survey. There were 44 species documented by Pearson (1933) that were also documented in at least one contemporary survey. There were 49 species that were not documented by Pearson (1933) but were documented in at least one contemporary survey.

Discussion

Bees Captured in Urban vs. "Natural" Areas. Urban areas in Chicago harbored a distinctive assemblage of bees, which differed somewhat from the bee fauna of surrounding natural areas. Bees collected at urban sites were largely native, widely-distributed species, and introduced exotics (Table 3). The bees collected most often at urban sites were peripheral members of the bee fauna represented in surviving areas of natural habitat. For instance, *M. rotundata*, a widespread introduced leafcutter bee, was often collected at urban sites. This species was present in Chicago Forest Preserves, including the Harms Woods

Table 5. Bee species documented in the survey by Tonietto et al. (2011) and in this survey.

Family	Species
Apidae	*Anthophora terminalis*
Apidae	*Apis mellifera*
Apidae	*Bombus bimaculatus*
Apidae	*Bombus fervidus*
Apidae	*Bombus griseocollis*
Apidae	*Bombus impatiens*
Apidae	*Ceratina dupla/calcarata*
Apidae	*Melissodes agilis*
Apidae	*Melissodes bimaculata*
Apidae	*Melissodes trinodis*
Apidae	*Peponapis pruinosa*
Apidae	*Xylocopa virginica*
Colletidae	*Hylaeus affinis*
Halictidae	*Agapostemon virescens*
Halictidae	*Augochlora pura*
Halictidae	*Halictus confusus*
Halictidae	*Halictus ligatus*
Halictidae	*Lasioglossum anomalum*
Megachilidae	*Anthidium manicatum*
Megachilidae	*Megachile centuncularis*
Megachilidae	*Megachile mendica*
Megachilidae	*Megachile montivaga*
Megachilidae	*Megachile rotundata*

Table 6. Chicago-area bee species documented in the survey by Pearson (1933) and in this survey or the survey by Tonietto et al. (2011).

Family	Species
Andreneidae	*Andrena cressoni*
Andreneidae	*Andrena imitatrix*
Apidae	*Apis mellifera*
Apidae	*Bombus bimaculatus*
Apidae	*Bombus fervidus*
Apidae	*Bombus griseocollis*
Apidae	*Bombus impatiens*
Apidae	*Ceratina dupla*
Apidae	*Ceratina stenua*
Apidae, Anthophorini	*Anthophora terminalis*
Apidae, Anthophorini	*Melissodes agilis*
Apidae, Anthophorini	*Melissodes bimaculata*
Apidae, Anthophorini	*Melissodes denticulata*
Apidae, Anthophorini	*Melissodes desponsa*
Apidae, Anthophorini	*Melissodes druriella*
Apidae, Anthophorini	*Melissodes trinodis*
Apidae, Anthophorini	*Svastra oblique*
Apidae, Nomadini	*Nomada articulate*
Colletidae	*Hylaeus affinis*
Colletidae	*Hylaeus mesillae*
Colletidae	*Hylaeus modestus*
Halictidae	*Agapostemon splendens*
Halictidae	*Agapostemon viriscens*
Halictidae	*Augochlora pura*
Halictidae	*Augochlorella aurata*
Halictidae	*Halictus ligatus*
Halictidae	*Halictus parallelus*
Halictidae	*Lasioglossum albipene*
Halictidae	*Lasioglossum anomalum*
Halictidae	*Lasioglossum coriaceum*
Halictidae	*Lasioglossum cressonii*
Halictidae	*Lasioglossum leucozonium*
Halictidae	*Lasioglossum pectorale*
Halictidae	*Lasioglossum pilosum*
Halictidae	*Lasioglossum zephyrum*
Megachildae	*Heriades carinatus*
Megachildae	*Megachile centuncularis*
Megachildae	*Megachile latimanus*
Megachildae	*Megachile mendica*
Megachildae	*Megachile montivaga*
Megachildae	*Megachile pugnata*
Megachildae	*Megachile texana*
Megachildae	*Osmia lignaria*
Megachildae	*Osmia pumila*

site, but was not often collected. For both urban gardens and railroad margins, the two species most often represented in our collections were introduced species. These include the honeybee, *A. mellifera*, which is actively cultivated by entrepreneurs and urban beekeeping enthusiasts, with public encouragement from city organizations, such as the Garfield Park Conservatory. Honeybees are well-represented in many nature preserves in Chicago, and Northern Indiana as well, though not as consistently nor in such numbers as in Urban Chicago. A series of hives kept by the Chicago Honey Co-op, fed entirely by open lot, garden, and railroad margin vegetation, produces honey commercially. Honeybee hives atop the Chicago Cultural Center supply the Lurie Garden and Art Institute with foraging *A. mellifera*. Also present in great numbers in these urban habitats was the introduced leafcutter bee, *M. rotundata*. Both of these species were collected at sites in natural areas as well, but were not nearly as conspicuous or numerous. A cosmopolitan bee of uncertain origins, the wool carder bee, *A. manicatum*, was also very common at urban sites, but inconspicuous or absent in preserved areas of natural habitat.

Notably absent from all the urban sites we surveyed were brood parasites of the genus *Nomada*, which were fairly conspicuous and diverse in wooded forests along the Des Plaines River. *Nomada* spp. invade nests built by bees of the genus *Andrena*, ovipositing their own eggs and displacing the larva of the host bee. The paucity of *Andrena* spp. hosts is likely to be the reason *Nomada* spp. were not collected at any urban site (though they were observed at the River Forest site, they evaded multiple attempts at collection). *Andrena* spp. were much less conspicuous and abundant in urban areas than in nature preserves. This large and important genus of bees contains a large number of univoltine and oligolecithic species, and all species in this genus build nests in sand, clay, and loosely-packed soil. The combination of these factors may render *Andren*a species poorly suited-for urban life. A large survey of New York City garden bees by Matteson et al. (2008) included not a single member of this genus, despite the high diversity of *Andrena* species in natural areas of New York State. In this light, it is interesting to note that some suburban areas near Chicago appear to be very friendly to *Andrena* spp. An interesting aggregation of *Andrena dunningi* (Cockerell), made up of perhaps 200 individual nests or more, occurs in the garden perimeter of a River Forest condominium, approximately 2 km from the Thatcher Woods site. In early April, males of this species were seen patrolling the loosely-packed, loamy soil of this site, periodically landing and searching for females. Females of this species were caught in the process of copulation with males. This aggregation has apparently persisted for many years at that site, and has been observed for three consecutive years by the authors of this study.

Andrena spp. were much more conspicuous at areas of preserved natural habitat, such as the Bunker Hill Savannah, the Harms Woods site, and the Indiana Dunes National Lakeshore. At these sites, *Andrena* spp. constitute a very important part of the bee fauna, sustaining populations of parasitic species of the genus *Nomada*. These floodplain deciduous forests at Harms Woods, and the Savanna at Bunker Hill, harbored oligolectic specialists, such as the small *Andrena wheeleri* Graenicher, which was frequently collected on Golden Alexander, *Zizia aurea* (L.).

Habitat Use. Ground-nesting, especially for bees requiring particular substrates, is quite possibly a factor limiting the ability of these bees to colonize urban areas. For instance, an eroding clay river bank at the Harms Woods site harbored a mixed species nesting aggregation of *Andrena* spp. (*A. dunningi* and another unidentified species), and their *Nomada* spp. parasites. Female specimens at Indiana Dunes National Lakeshore were often captured with fine grains of silica sand adhering to their forelegs and faces. Neither of these substrates, packed clay or fine silica, is typical of an urban environment. In their survey of urban garden bees in New York City, Matteson et al. (2008) note bees that nest in the ground are under-represented. Cane et al. (2006) studied the effects of habitat fragmentation on pollinator assemblages in Tucson, AZ. Their group concluded that some species responded positively to urbanization, and others did not. In their study, cavity-nesting bees, rather than ground-nesting species, were strongly favored in urban areas, presumably because urban habitats do not have appropriate nesting substrates for most ground nesting bees.

Even among bees that utilize holes, and holes of similar diameters, features of the natural history of some species make them better suited to urban life than others. Bees of the genus *Ceratina* Latreille were relatively conspicuous at the Indiana Dunes National Lakeshore, and in floodplain forests along the Chicago River, but absent from the urban areas we surveyed. These are very small bees that nest in small holes such as beetle borings, and urban gardens and railroad margins may lack nest sites of the appropriate size because beetle-infested trees are cut and cleared away. Unlike *Ceratina* spp., small bees of the genus *Hylaeus* (Fabricius) were common at many sites, in a wide variety of habitats. *H. affinis* and *H. modestus* occurred frequently in gardens. *Hylaeus* spp. utilize small twigs as a nesting substrate, and apparently can make do with a wide variety of habitats, provided twigs are present and flowers with a very small corolla length are also available. A small species of leafcutter bee (family Megachilidae), *Heriades carinatus* Cresson nests in small holes, and was similarly collected at both natural and urban sites, but small cavity nesters of another genus *Chelostoma* (Latreille), also members of the Megachilidae, were not.

Garden sites in Chicago harbored a considerable richness of bee species. Typically, gardens have higher floral diversity than open lots and urban railroad margins, and are more likely to have flowers continuously in bloom throughout the summer. This last attribute seems to make gardens especially attractive to bees. A common gardening practice at prestigous sites downtown is to plant dense collections of bulb flowers or other showy plants, and to remove them once the peak flowering time is over. The soil at these sites is continuously disturbed, and these areas were not well suited for bees. Catnip (*N. catara*), sunflower (*Helianthus annuus* L.), and foxglove (*Digitalis purpurea* L.) seem to be particularly useful to urban bees, as is sage (*Salvia officinalis* Linnaeus).

Native plants in a garden setting seem to be especially attractive to bees. The difference in species richness between urban sites harboring native vegetation, and those lacking native vegetation is substantial (Fig. 1). It is not known whether this effect is solely due to the presence of native plants, or is a side effect of greater floral diversity that seems to accompany sites where gardeners have made the choice to plant native species. Some of the patterns of resource use we documented seem to support the former possibility, however. At urban sites, native bees were captured more often on native flowers than on exotic flowers (Fig. 3). Oligoleges of the tribe Anthophorini, such as *Melissodes agilis* Cresson, *M. trinodis* Robertson, and *M tincta* La Berge, which specialize on sunflowers, were conspicuous and abundant at garden sites in late summer. Cultivated pumpkin plants, native but very far removed from their original ecological context, supported the oligolecithic squash bee, *Peponapis pruinosa* (Say), at Chicago garden sites. These bees, though abundant, can be elusive. The New York City bee survey by Matteson et al. (2008) failed to collect *P. pruinosa* in New York City, but the authors of that study made no special effort to visit squash blossoms early in the morning, which is the only reliable way of finding this bee when it is present.

Studies of other urban bee faunas have demonstrated that there is higher richness of bee species associated with native plants, as opposed to ornamentals, in Berkeley CA (Frankie et. al. 2005), and Phoenix, AZ (McIntyre and Hostelter 2001). In the Berkeley study, it was demonstrated that California native plants were much more likely to be visited by native bees (Frankie et al.

2005). In the Phoenix study, it was demonstrated that urban sites harboring native, xeric vegetation, harbored a higher diversity of bees than either natural desert sites, or urban sites harboring introduced mesic vegetation (McIntyre and Hostelter 2001).

Effects on Fauna of Forest Preserves. As for the question of whether widespread species typical of urban environments are a potential nuisance to adjoining areas of natural habitat, the problem seems to be restricted to a single species, *A. mellifera*. Honeybees are the only exotic collected in large numbers at sites in the forest preserve, and because of human intervention, this species seems to do well in a wide variety of ecological settings. The ecological effects of honeybees on native bees are hotly debated (Goulson 2003), and in Chicago, may have played out in the early nineteenth century. When it occurs, however, foragers of this species are almost inevitably present in very large numbers, for short periods of time when the utility of a floral source peaks. At Pinhook bog, an area valuable to conservation efforts because of its orchid populations, *A. mellifera* is so abundant during the spring, visiting the blueberry populations, that it is difficult for the authors of this study to imagine that honeybees have not impacted the populations of native species more suited to pollinate the native lady's slipper orchids, *Cypripedium acaule* Aiton at that site. *A. manicatum*, an aggressive competitor for floral resources, and highly territorial, was not well-represented in the forest preserves. Worth noting was the abundance of the bumblebees, *Bombus bimaculatus* Cresson and *Bombus impatiens* Cresson, at both urban and natural sites. It is possible that these two, widespread species have displaced local bumblebees more typical of the conserved habitats. In light of the widespread disappearance of *Bombus* spp., particularly *Bombus affinis* Cresson, a bee which was formerly very common in the Chicago area (Elizabeth Day, personal communication), it seems more likely that these two species are filling an ecological vacuum created by the decline of many native bumblebees, likely the result of introduction of the microsporidian *Nosema* sp., to North America (Winter et al., 2006).

Total Diversity and Comparison with Other Faunal Surveys. Bee assemblages are highly variable in time, possess a large number of rare species, and present many challenges to effective sampling (Williams et al. 2001). These factors make it very difficult to estimate the "true" number of species in any given area at any given time. Published surveys of bee fauna from North American urban areas have documented between 50 and 75 species. The total number of bee species from the Berkley, CA survey (74 species, Frankie et al. 2005), the Tucson, AZ survey (62 species, Cane et al. 2006), the Phoenix, AZ survey (54 species, McIntyre and Hostelter 2001), and the New York City Survey (54 species, Matteson et al. 2008) all fall within this range.

At the same time our team was collecting Chicago-area bees for this survey, a different survey was conducted by Tonietto et al. (2011). The two groups worked independently and were unaware of the other's efforts. The results of the two surveys invite comparison. Together, the two surveys present a much more complete picture of Chicago-Area bees. The combined list from these two studies includes 93 species of bees, in 27 genera, representing 5 families.

The redundancy of these faunal surveys presents an opportunity to examine the extent to which efforts of this sort are repeatable. Tonietto et al. (2011) conducted their survey over a single year, 2008. They chose six parks, six green roofs, six public gardens, and six prairies. Our survey took place over a greater span of time, with the first specimens captured as early as 2003. We chose railroad margins, public and private gardens, and areas of preserved natural habitat including dunes, wetlands, prairies, and floodplain forests. Nets and pan traps were used by Tonietto et al. (2011), whereas we used nets alone. Even given these differences, it is interesting to note how little overlap there is between the two species lists. The two groups collected only 24 species in common, out of a total list of 93 species. As noted in Table 5, the species listed in both surveys are common bees with broad geographic ranges. Williams et al. (2001) pointed out that bee assemblages contain many rare species and are prone to other difficulties in reliable sampling. The small overlap between the two species lists underscores this point.

Given the extensive reworking of natural habitat that has taken place since the early part of the twentieth century, it is of no small importance to know how the bee fauna of the Chicago-area has responded. In downstate Illinois, a very interesting before vs. after comparison was made by Marlin and LaBerge (2001) as they revisited a famous survey of Carlinville-area bees by Robertson (1928) that lists 297 species. Despite large-scale modification of the habitat in the vicinity of Carlinville, IL, 140 of species documented by Robertson (1928) were still present in 2001, plus 14 new species. Species of *Apis, Bombus*, and parasitic bees were not included in the survey by Marlin and LaBerge (2001), meaning that 140 of 214 species from Robertson's 1928 survey were recaptured.

In 1933, Pearson published an extensive survey of Chicago-area bees, representing thousands of specimens collected from a broad range of natural habitats present at the time. Comparing his list of 169 species to that of Robertson (1928), Pearson (1933) found that 157 of the bees he had documented in Chicago were also present in Robertson's survey.

Our results are not as encouraging as those of Marlin and LaBerge (2001). Of 169 species documented by Pearson (1933), only 44 were recaptured. Differences in sampling effort may partially account for this. Pearson (1933) collected many more specimens than two contemporary studies combined, our study and that of Tonietto et al. (2011). Perhaps a more likely scenario is that the Chicago Metropolitan area has undergone dramatic faunal change since Pearson's survey (1933). Pearson (1933) does not list his bee species by habitat; however, he does list the types of habitats he sampled. Clearly, he had free access to a broad range of natural habitats, including various types of dunes, prairies, and savannas. These same habitats, when present at all, are now restricted in scale, modified by human disturbance, and surrounded by an urban matrix of very dissimilar habitat.

Acknowledgments

Many thanks to Mike Arduser, who provided invaluable assistance in the identification of bees. Also, thanks to Elizabeth Day, who offered identification assistance as well, and to Tricia Stark, Manette Sandor, Marcus Thomasson, the Chicago Park District, the Chicago Forest Preserve District, The Indiana Dunes National Lakeshore, and Michael Thompson of the Chicago Honey Co-op.

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